Sigillariaceae of the Carboniferous in the Eastern Alps

Michael Wachtler
P. P. Rainerstrasse 11, 39038 Innichen, Italy; Email: michael@wachtler.com
Collaboration: Nicolas Wachtler; Email: nicolas@wachtler.com

Hardly any other fossil plant shows such a rapid rise to a giant tree and a decline to a dwarf plant as the family of the *Sigillaria*. Nowhere else can climate change, world catastrophes and ecological changes be marked out so well as with this clubmoss. Amazingly, *Sigillaria* came close to seed formation like the gymnosperms, and even their heterosporous fructifications were close to achieving the milestone of flowering. And yet, climate catastrophes hit them harder than other plants; although they were always ready to adapt and did mutate from giants to dwarf plants. Still, nothing helped: they died out without leaving any descendants, while apparently weaker plants still populate the Earth today. However, anyone who thinks that this common lycophyte has been reasonably well researched is wrong. On the basis of numerous *Sigillaria* finds of the Upper Carboniferous in the Eastern Alps, especially the widespread *Sigillaria parallela,* an attempt is made to reconstruct the development, the peculiarities and the reproductive properties of these clubmoss and to show that they themselves triggered major climatic catastrophes.

March 2023
Keywords: Upper Carboniferous, Alps, Lycophyta, *Sigillaria*

Upper Carboniferous, Kasimovium-Gzhelium. *Sigillaria parallela* landscape (Königstuhl)
Left: you can see a *Sigillaria* tree with its cone-shaped fructifications; below, a seedling is present; **Middle:** A rotten tree is present; **Right:** Remains of fertile and sterile parts protrude into the picture. The sporophylls have been shed.

The frequent occurrence of giant clubmoss trees in the Late Carboniferous has fascinated researchers since the beginning of paleobotanical research. They became synonymous for an entire epoch, capturing people's imaginations with everything associated with monumental growth, from huge insects to gigantic plants.
The first of the two most widely known clubmoss, *Lepidodendron,* was first described in 1820 by Count Caspar Sternberg, using stem fragments with *"rhomboidal leaf cushions",* considered to be taller rather than wider *(Lepidodendron aculeatum)*. The second giant clubmoss, *Sigillaria (scutellata)*, followed two years later in 1822, and was described by the father of French paleobotany, Adolphe Brongniart (1801–1876). Elliptical to round imprints on the bark (as a result of shed leaves) were a characteristic feature of this clubmoss group.


Sigillaria Deutschiana AdBr. . . . . Saarb
Sigillaria parallella Mihi. . . . .
Neuropteris cordata Ad. . . . . Alais

Filices.

*) Plantae herbaceae v. arborescentes vegetatione terminali crescentes.
Fasciculi vasorum scalariformium serie unica in formam retis cylindrici medullam includentis complexi, e cujus parte exteriore nec non interiore fasciculi accessi in folia radicesque transeunt.
Sporangia in foliorum dorso vel margine nidulantes.
Porosus *Cotta*. Protopteris *Corda*. Tubicaulis *Cotta*. Caulopteris *Lind*. Karstenia *Göpp*. Cottaea *Göpp*. Sigillaria? *Brong*.

SIGILLARIEAE. 127

56. Sigillaria parallela UNG. *Ueber ein Lager vorw. Pfl. p.* 150.
In anthracite alpium Stangalpe Stiriae.

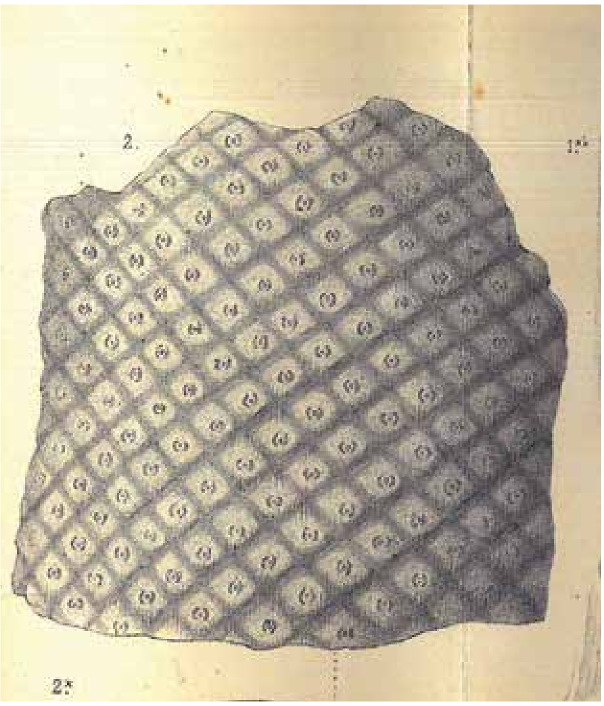
In "*Ueber ein Lager Vorweltlicher Pflanzen auf der Stangalpe in Steiermark" (About a Site of Prehistoric Plants on the Stangalpe in Styria,* 1840), Unger described a new species of *Sigillaria* under the name *Sigillaria paralella.* In his description, written in Latin, he placed them with the Filices, i.e. the ferns. In the 1847 paper "*Chloris Protogaea. Beiträge zur Flora der Vorwelt" (Chloris Protogaea. Contributions to the Flora of the Prehistoric World),* Unger classified them under the club moss.


The Austrian paleobotanist Franz Unger was the first to research the East Alpine sites relevant to the Carboniferous (Archive Dolomythos Museum).

The extraordinary preservation and the number of the giant lycophyta from the Upper Carboniferous of the Eastern Alps, especially of the main families *Sigillaria* and *Lepidodendron*, fascinated both researchers and other interested people. Where else was it possible to follow many different fossil-rich layers over hundreds of meters! However, the remoteness of the high alpine sites, which required long hikes, posed a disadvantage that could not be underestimated. This fact, and the frequent lack of interest in paleobotanical study today, ensured that these arboreal lycophytes – which inhabited the Earth more than 300 million years ago – would remain among the least studied fossil plants.

Historical overview

The richness of fossils, especially from the Stangalpe and the Königstuhl in the Carinthian Nockberge, was first superficially described in 1779 by Bishop Sigismund von Hohenwart (1745–1825) and later in 1835 by the German-Austrian geologist and physician Ami Boué (1794–1881), who gave a list of various plant fossils such as clubmoss, horsetail and ferns (Fritz, 1990). It was the founder of Austrian paleobotany Franz Unger (1800–1870) who researched


In the work *"Anthracit-Lager in Kärnten" (Coal-field in Carinthia)* published by Franz Unger in 1870, he depicted *Sigillaria* stems under the name *Semapteris tessellata (*Plate III, Figure 2) (Archive Coll. Wachtler, Dolomythos).

these areas more intensively; he not only described them in several publications (Unger, 1838, 1850, 1870) but also made his collections available to other researchers such as Caspar von Sternberg, who in turn was the first to name several plant fossils such as *Neuropteris alpina* or *Cyclopteris alpina* from the Stangalpe (Sternberg, 1838).

In the 1840 publication *"Ueber ein Lager vorweltlicher Pflanzen auf der Stangalpe in Steiermark"*, Unger mentioned various petrified plants, including ferns such as *Pecopteris,* horsetails (*Calamites*) and clubmoss *(Lepidodendron, Sigillaria),* but their illustrations did not exist; even the descriptions and new mentions were missing or were dealt with in a few Latin words. Unger seemed overwhelmed by the amount of plant parts found and, therefore, he introduced a large number of new genera and species.

Nevertheless, his writing (in the style of the time) provides a pleasant description of the events and experiences gathered from his hikes to the Stangalpe in the years before: *"Wem die Entdeckung dieser dem Geognosten eben so wie dem Botaniker höchst ansprechenden Grabstätte einer vorweltlichen Flora gebührt ist nicht bekannt" (Who is responsible for the discovery of this burial site of prehistoric flora, which is equally appealing to the geognostic as well as to the botanist, is not known),* Unger states, adding that *"wahrscheinlich sind Hirten und Jäger auf die sonderbaren Zeichnungen der auf den Alpen herumliegenden, theilweise verwitterten Thonschieferplatten zuerst aufmerksam geworden"* (*probably shepherds and hunters first became aware of the strange drawings on the partially weathered clay slate slabs lying around in the Alps)* (Unger 1840, p. 140). Unger visited the Stangalpe twice, but due to the lack of time, he was only able to carry out cursory scientific investigations. He also mentioned receiving most of his specimen for examination from the then-mine-director Peter Tunner.

Proposal for solving the nomenclature

The high-alpine sites enable the tracking of different layers deposited at different times over long distances and also the elaborate on the seasonal differences. Particularly, fossil sites already known around 1800, such as the Stangalpe and the Königstuhl in the Nockalm area (in the borders of Carinthia, Salzburg, Styria), as well as some localities in the Carnic Alps (here in particular the Kronalm on the Austria-Italy border ridge), prove to be particularly fruitful in this regard.

Now, a fundamental question arises: how can the *Sigillaria* remains on the Kronalm, the Stangalpe, and especially those on the eastern ridge of the Königstuhl, in the direction of the Rosaninscharte, be classified? Certainly not with the large number of names that Franz Unger already gave (1840, 1847, 1870); by 1847 alone, he had already mentioned 147 different species. Other authors adopted this list and generously extended it (Štúr, 1871; Zwanzinger, 1872, 1876, 1891; Jongmans, 1938; Berger, 1960; Fritz & Boersma, 1988; Fritz et al., 1990; Kabon, 1997; Kabon & Amerom, 1999). Around 1880, more than 300 species were counted, and in 1904 the German researcher Werner Koehne came up with 408 different *Sigillaria* species only in Europe.

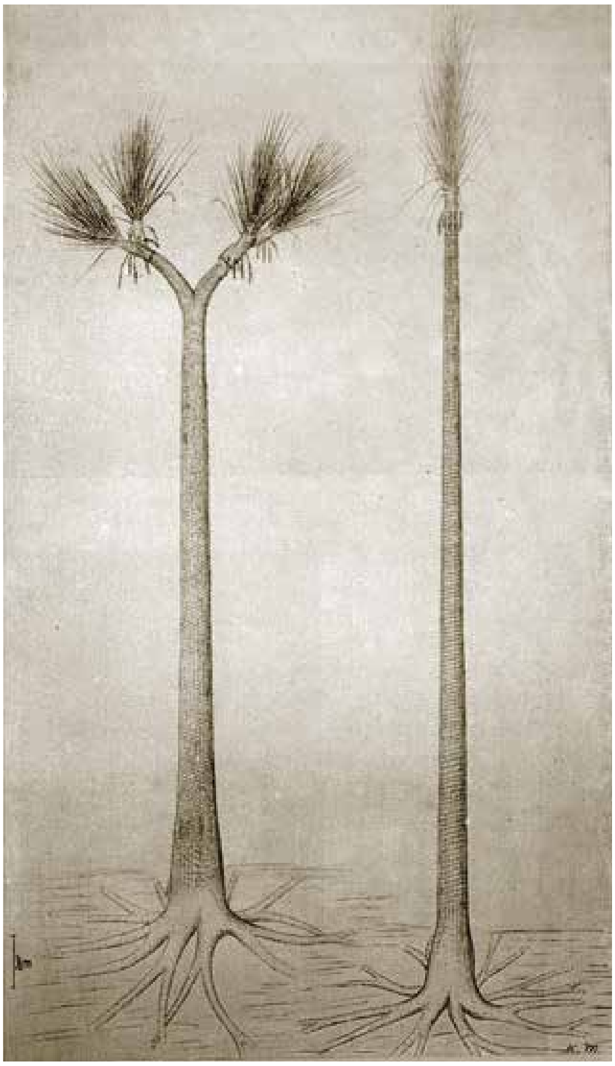
In addition, the plant parts described under different names such as *Knorria* (bark impression), *Syringodendron* (inner stem impression), *Sigillariostrobus* (fertile parts), *Sigillariocladus* (leaves), *Stigmaria* and *Stigmariopsis* (roots) were added, with no clear assessment of whether they belonged to the other giant clubmoss *Lepidodendron*. The number of species continued to grow as a result, so that in the end the lycopod trees grew into the most confused witnesses of paleobotanical research, and the scientific task of conveying knowledge receded into the background.

Sigillaria parallela

However, in addition to the various *Sigillaria* (*Sigillaria leioderma, S. defrancii, S. brardii, S. gracilis,* etc.) obtained from other European localities, Unger, from the Stangalpe, mentions a *'Sigillaria parallela'.* Although it was first described in 1840, on the verge of incompleteness, and even provided with an incorrect orthographic designation as *Sigillaria parallella,* we still received a first indication of this species, since it represented the only new description of a *Sigillaria* from this area. Unger corrected the grammar in 1847 to *Sigillaria parallela,* so that this species name perhaps best corresponded with the original wishes and thoughts of the first author. However, in the 19th century, it was hardly possible to bring larger stems from the heights of the Nockalm peaks or the Carnic Alps down into the valley areas.

Even today the description of *Sigillaria* remains complicated, owing to the fact that Unger edited a publication in 1870 (the year he died) under the title *'Anthracit-Lager in Kärnten'* with three plates, where he described another *Sigillaria* with the newly introduced generic name *Semapteris tesselata,* in addition to other ferns. On Plate III, Figure 2, there were references to stem parts belonging to the *Sigillaria* obtained from the Kronalm in the Carnic Alps.

Unger's considerations remain hardly comprehensible today. Adolphe Brongniart described a *Sigillaria tesselata* in 1822; this did not prevent Unger from renaming it *Semapteris tesselata*, since he felt that there were differences: *'Die Verwandtschaft dieses Petrefactes mit Sigillaria Brardii Brong., weniger mit Sigillaria Serlii Brong., ist nicht zu übersehen, doch fehlen unserer Pflanze die scharf umschriebene Narbenfläche,....abgesehen davon, daß auch die Gefäßbündelnarben nicht vollkommen untereinander übereinstimmen' ('The relationship of this Petrefactes with Sigillaria Brardii Brong., less so with Sigillaria Serlii Brong., cannot be overlooked, but our plant lacks the sharply defined stigma surface,.... apart from the fact that the vascular bundle scars do not completely correspond with each other').* This was an extremely poor justification, because he explained the classification as *Semapteris* with similarities to a possible fern trunk.



Former reconstructions of *Sigillaria:* left, the dividing subgenus *Favularia*; right, *Eurhytidolepis* (Mägdefrau 1956). These widely used illustrations ignored the fact that the trunks, often more than a metre wide, could hardly have been built up with such scant tufts of leaves on the crown.

The actual complexity of the matter became evident in light of the *Semapteris carinthiaca* described by Franz Unger in 1870, which in principle represented a *Sigillaria carinthiaca*. Another *Sigillaria carinthiaca* from the Nötscher Karbon, with the same name, was documented by Kabon and Ameron in 1999 as a new species.

Hence, the first basic question is, whether the appearance and structure of these *Sigillaria parallela*, which differ slightly in age between the Kronalm and the Nockberge fossil sites, differ so much so that they can be split up into different species. Since the aim of paleobotanical research must be to pass on knowledge and not to fall into quibbles, the answer to this question should be 'no': the differences in the leaves, stems and especially the fructifications are too small to be deemed important. Thus, until a final clarification is made, the name *Sigillaria parallela* must be deemed the most appropriate with respect to these Eastern Alpine localities.

Attempt to decipher a riddle

However, the assumption that at least *Lepidodendron* and, to a greater extent, *Sigillaria* have been well researched, judging by the large number of publications, is unsatisfactory. There are still large gaps in our knowledge of the blueprint of this plant, added to even more confusion about its reproductive properties.

Hardly any other fossil plant genus reveals the knowledge situation to be so opaque. Even with the hundreds of descriptions of *Sigillaria* species as early as the 19th century, mostly associated with a lack of illustrations or with leaves and sporophylls put in an overall context, hardly any attempt was made until the late 20th century to solve or simplify this Babylonian confusion. Even the reconstruction drawings, which are always the same, hardly stand up to scrutiny: often the main stems, thicker than 1 m, are combined with a tree crown supplemented by two measly tufts of leaves, in a figure that does not qualify for any scale comparison.

In finding the solution to this enigma, the unusual *Sigillaria* structure composed of several layers of different nested trunks (like a Russian doll) proves to be an obstacle, as the upper and lower parts of the stem differ considerably in appearance, and the root


By 1904, Werner Koehne had already listed 408 species of *Sigillaria*, as well as additional parts such as *Syringodendron* (inner stem), Sigillariostrobus (fertile parts), *Sigillariocladus* (leaves), *Stigmaria* and *Stigmariopsis* (roots). Images: List of the different types of *Sigillaria* by Werner Koehne.

The classic site of the Stangnock seen from the Königstuhl. The layers rich in plant fossils are placed in a band at the lower centre. The strata are rich in *Sigillaria, Lepidodendron* and seed ferns. Everywhere, powerful fire layers can be found (Michael Wachtler, 2007).

The site on the eastern ridge of the Königstuhl is rich in mighty *Sigillaria* trunks, which are overlaid by charcoal fire horizons.

strands, which can be confused with above-ground trunks, has caused generations of scientists to despair. To further complicate the research, while rotten trunks from the Carboniferous swamps are found in large numbers, trees standing in sap with connected foliage are rare.

Exacerbating the problem of assignment, both *Lepidodendron* and *Sigillaria* reportedly have relatively similar narrow, elongated leaves with a prominent midrib. Furthermore the Sigillariaceae are externally characterised by mostly similar sporophylls, with megasporophylls bearing only one huge sporangia and microsporophylls encasing lots of microsporangia. Also, the interpretation of the rarely-occurring intact sporophyll cones is even more difficult, so that despite 200 years of research hardly any concomitant successes worth mentioning have been achieved.

In the beginning of 2000, Georg Kandutsch and Michael Wachtler started further attempts to re-evaluate the giant clubmoss flora of the Eastern Alps. Kandutsch managed to transport an intact lower part of the outer bark, with a diameter of one meter, from the Königstuhl down into the valley. On the same slab there was another massive trunk, this time with a partially peeled-off bark.

As a result, Michael Wachtler uncovered further trunks from the same layer, which, due to the attached leaf parts, belonged to a middle-to-upper part of a *Sigillaria* stem standing in sap. These trunks were around 70–80 cm in diameter. Other parts of the tree from the upper trunk areas were surrounded by a large number of narrow leaves up to 30–50 cm long, with a typical median nerve. These were the rarely found, non-rotting trunks of a *Sigillaria*. Even the forking branches from the apical area as well as the parts of the plant

One-meter-wide basal S*igillaria* stem with a bulging bark, from the Georg Kandutsch Collection (Nockalm Museum). On the right is another trunk, the outside bark has been partially peeled off.

in sterile (rather than fertile) form came to light, which allowed the completion of the overall picture of the plant.

All of these reconstruction attempts, especially regarding the fructifications, would have been in vain if Michael Wachtler (2016) had not succeeded in recovering the last descendants of the Sigilariaceae in excellent condition (*Sigillcampeia nana)*, from Lower Middle Triassic layers (Anisian) of the Dolomites. Prior to his findings, it was assumed that the *Sigillaria* died out in the course of the Permian, with their last representative being *Sigillaria brardii.* Surprisingly, however, some representatives survived across the Permian-Triassic boundary and recovered throughout before completely dying out.

The dwarfism of these plants in the Triassic – with a total height of only 20–40 cm – made it possible to reconstruct the structure of *Sigillaria*, especially the fertile parts, divided into macrosporangia and microsporangia. Interestingly, the *Sigillaria* lost wood volume and size over the Permian to the Early Triassic, whereas the sporophylls and the leaves retained their size. The many dichotomizing branchlets reduced from a numerous presence in the Carboniferous to a simple bifurcation in the Triassic.

The rise and fall of the Sigillariaceae can be documented in the Alps over a period of almost a 100 million years – from the Carboniferous through the Permian and over almost the entire Triassic – and the related statements about massive climate changes, fire catastrophes covering entire continents or the sudden appearance of better-adapted plants, such as the gymnosperms, can be made.

The focus of this work is on the Upper Carboniferous *Sigillaria parallela*, which was described by the Austrian paleobotanist Franz Unger in 1840, from the Stangalm area in the Nockberge, although the description was extremely inadequate. Obtaining deeper knowledge about these plants based on fossil finds can be a milestone in paleobotanical research, because only then can an important question be clarified – that of the classification and appearance of this giant clubmoss.

Systematics

Class Lycophyta
Genus *SIGILLARIA* Brongniart 1822

Sigillaria parallela Unger 1840

1840 *Sigillaria parallella*, UNGER, p. 127
1847 *Sigillaria parallela*, UNGER, p. 56

Neotype
KOEN 235, Königstuhl, Coll. Wachtler, Dolomythos Museum, Innichen

Geological age
Upper Carboniferous, Kasimovian-Gzhelian

Material
Sigillaria parallela is mainly found on the east side of the Königstuhl (Nockalm area), in the direction of the Rosaninscharte, somewhat less frequently on the nearby Stangnock and frequently, in some lenses, on the Kronalm in the Carnic Alps.

Etymology
The original name "*Sigillaria parallela*" was assigned in 1840 by the Austrian paleobotanist Franz Unger, probably due to the characteristic parallel, elongated bark pattern of this plant.

Description
Tree: Mature trees reached a growth height of probably 20–30 m with a trunk circumference of 1 m or more. The root area (often described as *Stigmaria* in the literature) consisted of flat roots with forked main axes, from which many hollow secondary roots branched off (KRON 306, KRON 281, KRON 240, KRON 295, KOEN 200). The appearance of the stems varied greatly and, in the past, had often given rise to interpretations and different namings. The lower part of the stems was often covered by a furrowed-to-fissured bark (KOEN 01, KON 290) *(Knorria*), while the upper part either showed stem segments covered with leaf scars or parallel-running smooth ribs from underlying areas (*Bergeria, Aspidaria*), depending on the state of preservation. Since the stem consisted of horizontal ribs lying close together, presumably the main trunk of the Sigillaria could be an arrangement of closely fused individual stemlets of 1–2 cm thickness (KOEN 04, KOEN 269, KOEN 26, KOEN 28, KOEN 24, KRON 286, KRON 284, KRON 229, KRON 315, KRON 244).
This view was supported by the seedlings, from which closely spaced, dichotomously forking branchlets developed around a single protostele. Some stronger vascular bundles branched off again and again to form plectostelae. The trunk of the *Sigillaria* was, therefore, considered as nothing other than an assemblage of many protostelae growing together (KRON 382).
Branches and leaves: Since most of the *Sigillaria* recovered were leafless stems, it was assumed that they were characterised by a low proportion of chlorophyll-forming leaves. This view (Mägdefrau, 1956) was probably due to the fact that most of the clubmosses found were composed of fallen, rotted plants which were fossilized in that way. Stems from the Königstuhl proved (KOEN 305), however, that *Sigillaria* from the upper half of the trunk was densely covered with leaves, some of which were up to 50 cm long and narrow, with a prominent central rib (KOEN 17, KOEN 224, KOEN 222, KOEN 278, KRON 202, KRON 260, KRON 204).
In the crown, *Sigillaria* bifurcated many times – in contrast to the general opinion (Taylor et al., 2009) – into a multitude of widely spreading lateral branches covered with long leaves. Just like the main stem, the side branchlets lost their foliage (KRON 439, KRON 211, KOEN 32, KOEN 268, KOEN 152), so that mostly side branches with typical, spirally arranged, rhombic-to-elliptical leaf cushions were often preserved, further characterised by two-three slightly downward-curved punctiform scars (*Sigillaria parallela).* Moreover, they were only rarely recognisable.
Fertile organs: Even more complex than the structure of the sterile plant was the knowledge about the appearance of in-

***Sigillaria* fire horizons**

1–2. On the eastern ridge of the Königstuhl, layers rich in *Sigillaria* can be traced over many meters. Repeatedly, there are huge layers of ash, bearing a legacy of massive fire disasters; 3–4. The same phenomenon occurs at the Kronalm. Here, too, there are considerable fire horizons over *Sigillaria* trunks.

fructescence, which was either not dealt with in the literature or was given inconsistently. Even a standard work of paleobotanical research, *'Paleobotany. The Biology and Evolution of Fossil Plants' (*Taylor et al., 2009) mixed the fructifications of *Lepidodendron* with those of *Sigillaria* or other Paleozoic lycophytes. This must be overlooked, since complete sporophyll stands are extremely rarely found and can even then be mistaken for shortened sterile leaves. Only through the mass occurrence of the Triassic dwarf Sigillariaceae *(Sigillcampeia)* could the structure and appearance of the infructes-

Sigillaria parallela. seedlings. Kronalm (Upper Carboniferous)

1. Seedling; 2–3 Seedling with branching plectostelae, as well as details of a forking main axis; 4. Seedling with a branching protostelae (all KRON 382); Coll. Wachtler, Dolomythos Museum, Innichen.

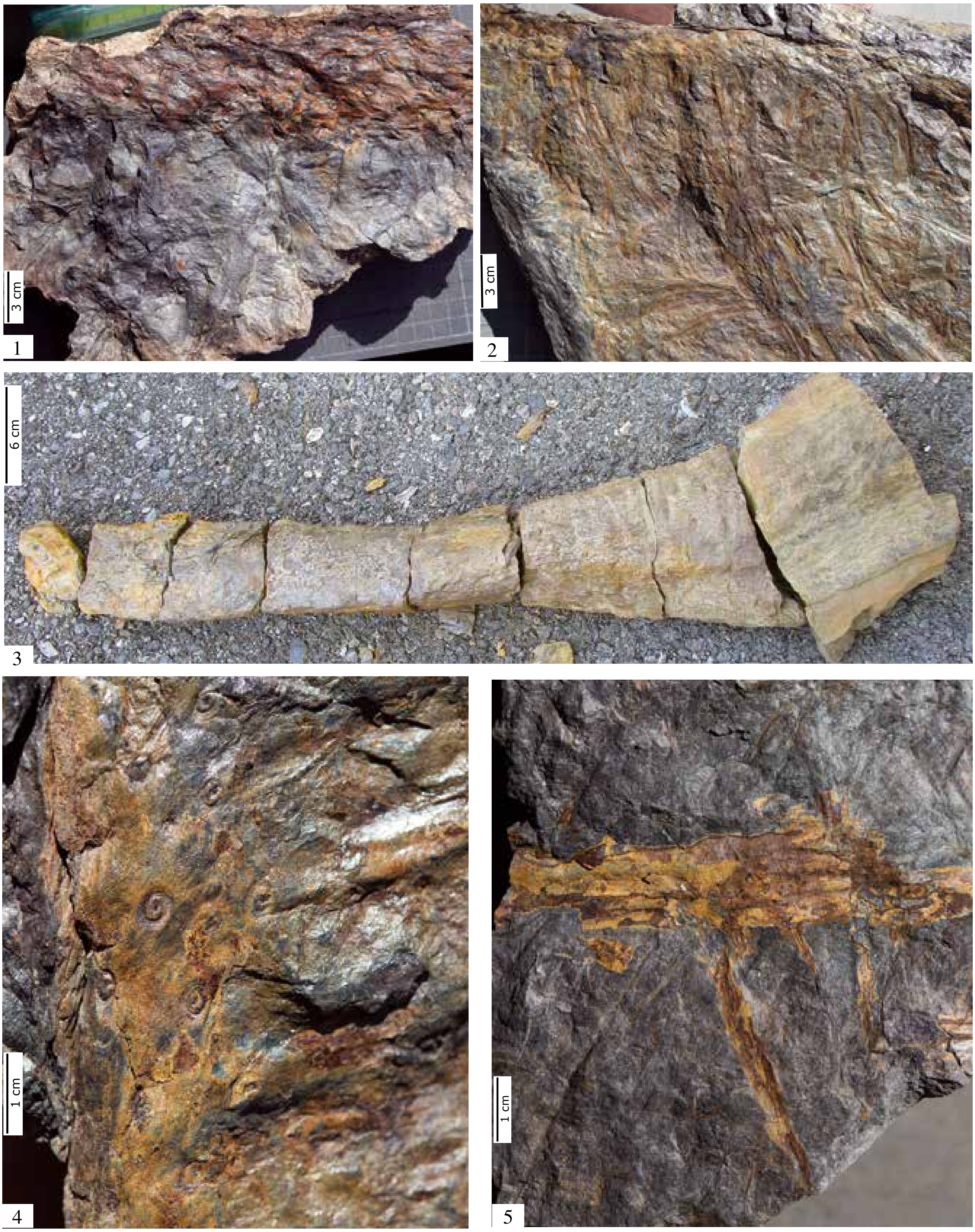
cence, as well as the associated megasporangia and microsporangia, be made comprehensible (Wachtler, 2016).
The strobili were heterosporous 'cones' reaching up to 20 cm (KOEN 235, neotype, KOEN 181, KRON 278), carrying two different types of sporophylls but being similar in size. The megasporophylls grew in the lower part of the infructescence (KRON 314, KRON 224, KRON 271, KRON 217, (KRON 358, KRON 305, KRON 279, KRON 217), the microsporophylls in the upper part (KOEN 285, KOEN 204, KOEN 241, KRON 212, KRON 210, KRON 208, KRON 275, KRON 275, KRON 181, KRON 242, KRON 341, KRON 218).
It is interesting that the megasporophylls developed only one, large, round macrospore, while the microspores settled in hundreds in slightly elongated microsporophyll cavities. On the upper side of the plant, a thin ligule prevented the sporangia from falling out while growing, while on the underside the sporangia were attached to a leaf-shaped, sterile, elongated and tapered bract, which could protrude far beyond the sporangia. In this, they resembled some Paleozoic conifers, such as *Wachtlerina* or *Majonica* and (partly) also today's fir conifers, with the exception that the gymnosperms would form monoecious cone structures, (i.e. with different male and female cones), while the Sigillariaceae, surprisingly, would make their way up to the seed formation but remain heterosporous. This caveat could also evoke associations with flowering plants, although the basic structure of the infructescence would be fundamentally different and originate in another way.
The terminal sporophyll cone disintegrated after maturity, with both the bracts and the megasporangia or microsporophylls becoming independent. Plus, the slightly flatter and elongated microsporophlls released their microspores through openings in the upper part. Sometimes, entire layers of fossil microspores were found in the sediments, showing triangular ornamentation under good preservation conditions.
The megasporangium, composed of different cell walls and about 2–2.5 cm in size, showed a characteristic opening in the upper part into which the microspores could enter. They were sometimes described as seed clubmosses in the past; this seems entirely justified. It would also be necessary to investigate in more detail whether those macrosporangia described as *Lagenostoma lomaxii* (Taylor et al. 2009) and previously associated with the seed fern genus *Lyginopteris* could not better be classified as belonging to *Sigillaria*. In most cases, however, they were given generic names such as *Lepidocarpon* (Taylor et al., 2009), although the name *Sigillarocarpon* would make more sense, because the Lepidodendrales had a different structure in their homosporous sporophyll states. However, considerable ambiguity still exists here, especially because a myriad of names have been introduced, such as *Mazocarpon* or *Sigillariostrobus,* and these have been associated with sporophyll cones hanging from the tree (DiMichele, 1980) instead of being related to all extant lycophyta with upwards growing fructifications.
Coming back, as soon as the microsporophylls and macrosporophylls fell off, the typical elongated, sometimes wavy scars remained on the plant's sporophyll stands. While the cushions of scars from *Sigillaria parallela* at the (probably) geologically slightly older sediments from the Königstuhl were still encased by a dense accumulation of many tiny, sterile micro-leaflets in the basal part (KOEN 235, neotype, KOEN 291, KOEN 215, KOEN 154, KOEN 142, KOEN 207), the probably younger layers on the Kronalm (KRON 296, KRON 265, KRON 311, KRON 304) and, to a greater extent, *Sigillcampeia* from the Triassic managed to form an inseparable unit, with no more recognisable dwarfish leaflets. Thus far, this was one of the few differences between *Sigillaria parallela* from the Königstuhl and from the Kronalm.
The Sigillariaceae could thus be fertilized both on the sporophyll cone and later, when they would float in the swamps, whereby the small microspores could be carried over long distances, in which case the radius of the megasporangia must have been smaller. The crop rotation was, therefore, much more like that of today's *Selaginella* clubmoss rather than that of the extant *Lycopodium.*

Catastrophic forest fires and the flourishing of the *Sigillaria*

Interestingly, the remnants of catastrophic forest fires can be found in the strata

***Sigillaria parallela*. Roots (Upper Carboniferous)**

1–2. Roots with hollow leaf scars (KRON 306); 3–4. Root area with torn-off secondary root scars (KRON 281, KRON 240); Coll. Wachtler, Dolomythos Museum, Innichen.



***Sigillaria parallela*. Roots (Upper Carboniferous)**

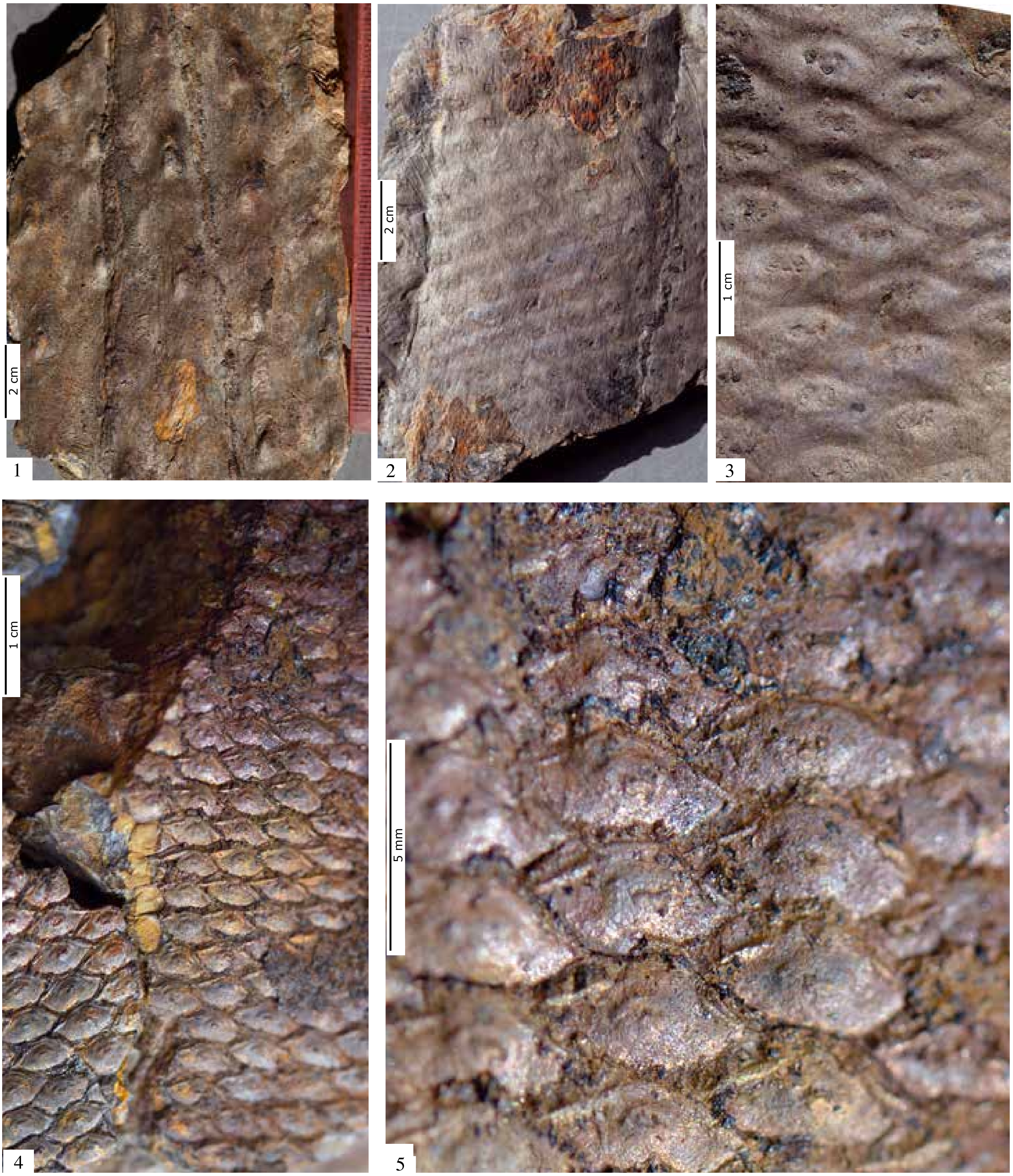
1–2. Root systems with branching secondary roots (KRON 295, KOEN 200); 3. Detail of a main root (Coll. Perner); 4. Main root (called Stigmaria in the literature) with cushions of shed and attached secondary roots (KOEN 200); 5. Detail of a secondary root (KOEN 188); Königstuhl, Coll. Wachtler, Dolomythos Museum, Innichen.

Sigillaria parallela. Various details of the main stems. Königstuhl (Upper Carboniferous)

1. Bark layer from the lower part (KOEN 01) (Described in the literature as *Knorria)*; 2. Inner layer of a trunk (KOEN 04); 3. Upper part of a trunk with parallel axes (KOEN 269); 4. Upper, inner part of a trunk (KOEN 26); 5–6. Upper part of a stem and details of the leaf scars (KOEN 28, KOEN 24); Coll. Wachtler, Dolomythos Museum, Innichen.

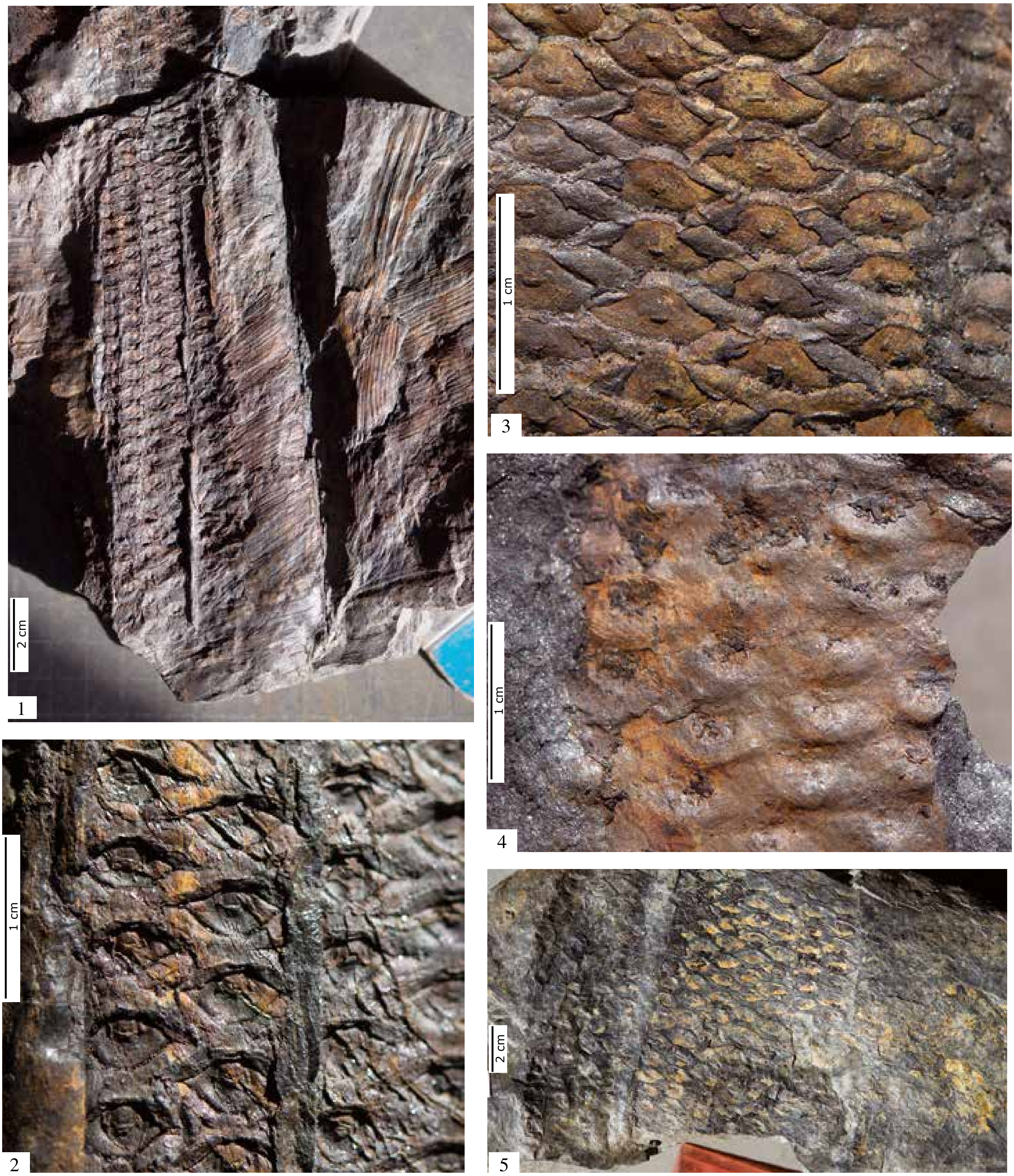
***Sigillaria parallela*. Various details of the main trunks. Kronalm (Upper Carboniferous)**

1. Lower part of a trunk (KRON 290); 2. Lower part of a stem with the preservation of the inner and outer bark (KRON 286); 3–4. Lower parts of stems (KRON 284, KRON 229); 5. Apical inner part of a stem (KRON 315); 6. Upper part of a trunk (KRON 244); Coll. Wachtler, Dolomythos Museum, Innichen.



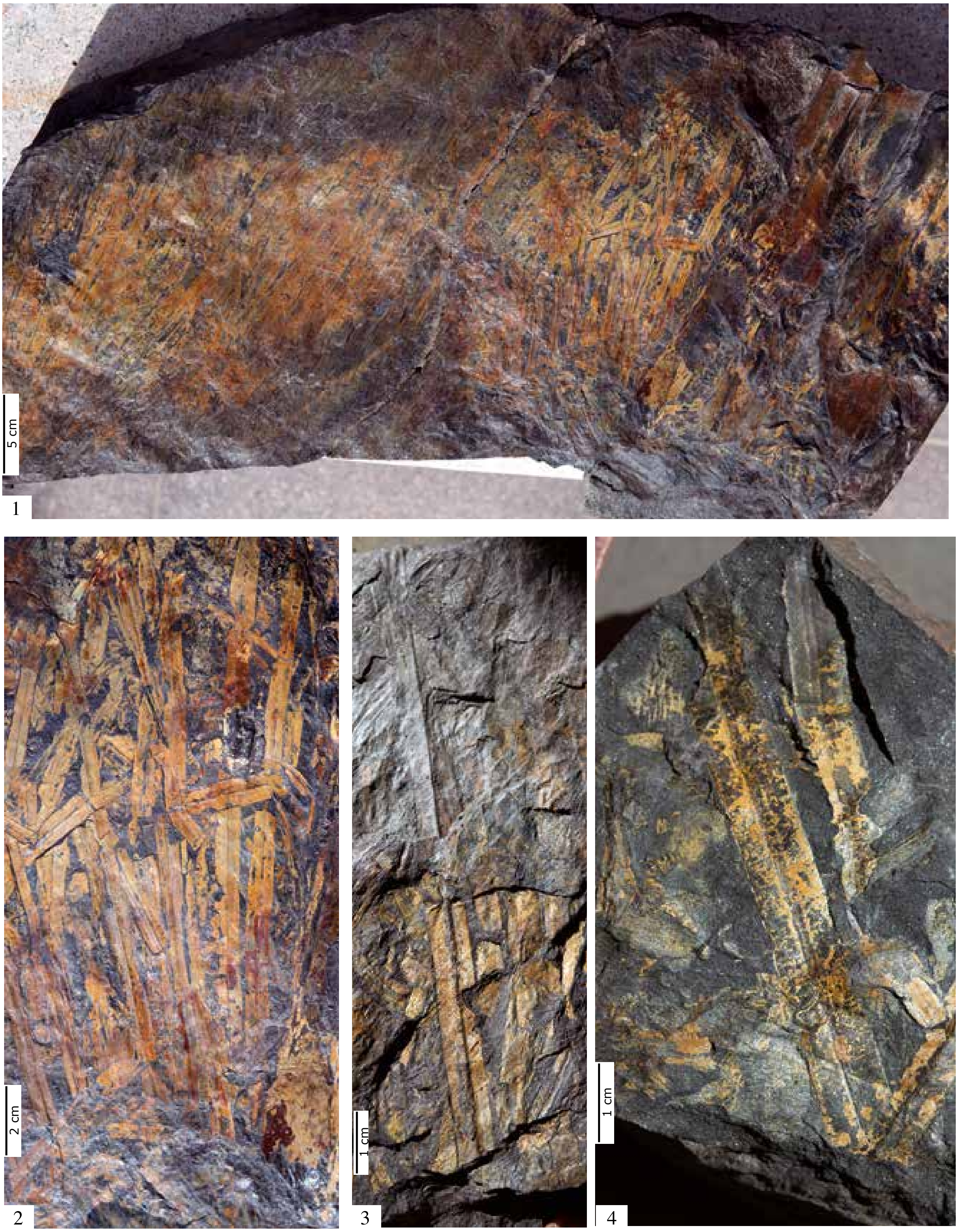
***Sigillaria parallela*. Various details of the canopy. Kronalm (Upper Carboniferous)**

1. Apical parts of the side branches (KRON 288); 2–3. Apical parts of the branchlets and detail (KRON 439); 4–5. Apical branches with details of the leaf scars (Coll. Perner, Dolomythos Museum, KRON 211); Coll. Wachtler, Dolomythos Museum, Innichen.



***Sigillaria parallela*. Various details of the canopy. Königstuhl (Upper Carboniferous)**

1–2. Apical parts of side branches with details of cushions from fallen leaves (KOEN 32,); 3–4. Various conservation examples (KOEN 268); 5. Side branch (KOEN 152); Coll. Kandutsch (1-2), Coll. Wachtler (3-5), Dolomythos Museum, Innichen.

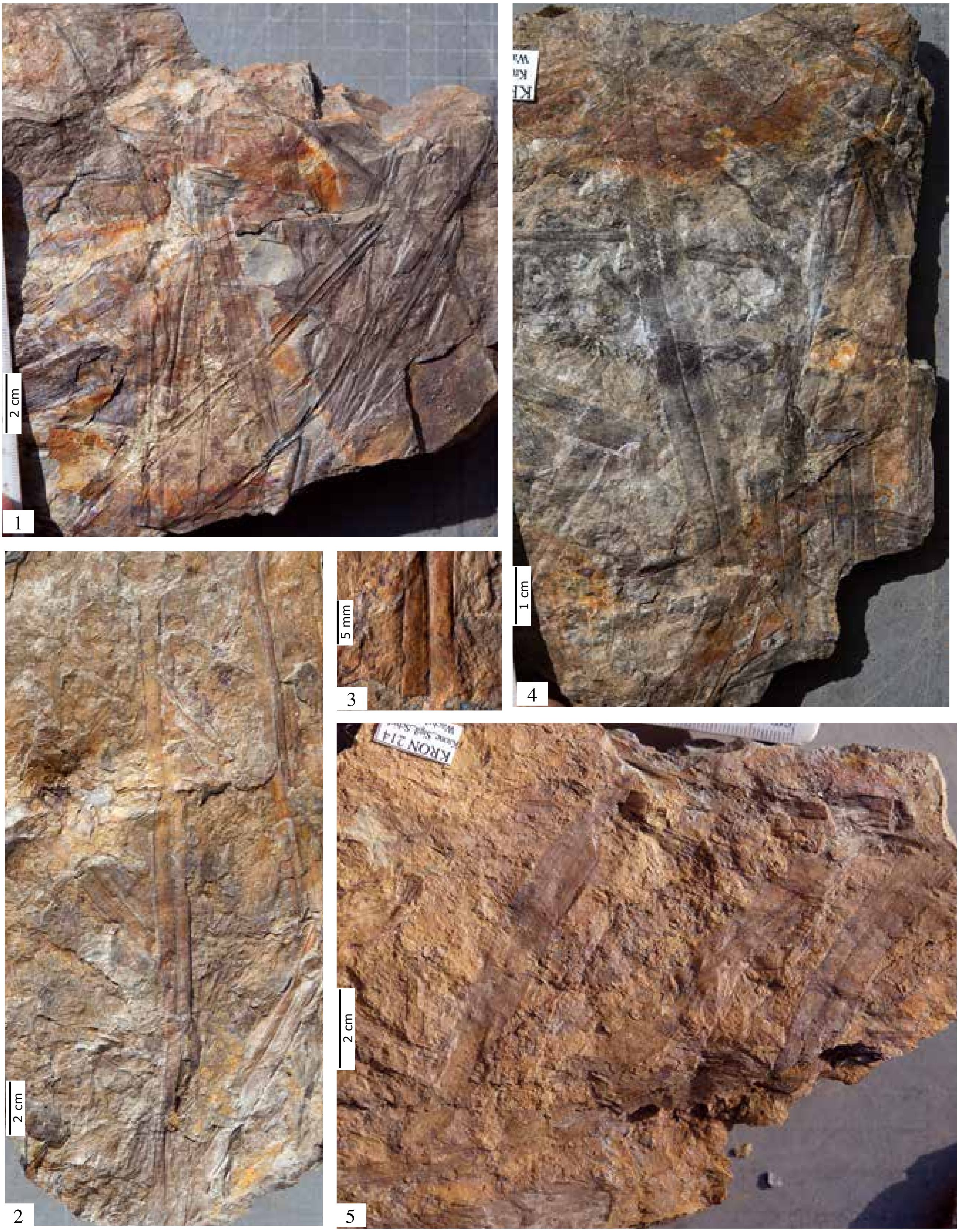


***Sigillaria parallela*. Leaves and stem parts. Königstuhl (Upper Carboniferous)**

1–2. Large plate with Sigillaria-leaves (KOEN 305); 3. Detail of leaves with midrib (KOEN 17); 4. Detail of a creased leaf (KOEN 224); Coll. Wachtler, Dolomythos Museum, Innichen.

***Sigillaria parallela*. Leaves. Königstuhl (Upper Carboniferous)**

1–2. Various leaves and details of the prominent midrib (KOEN 222); 3–4. Detail of a creased leaf (KOEN 278); Coll. Wachtler, Dolomythos Museum, Innichen.

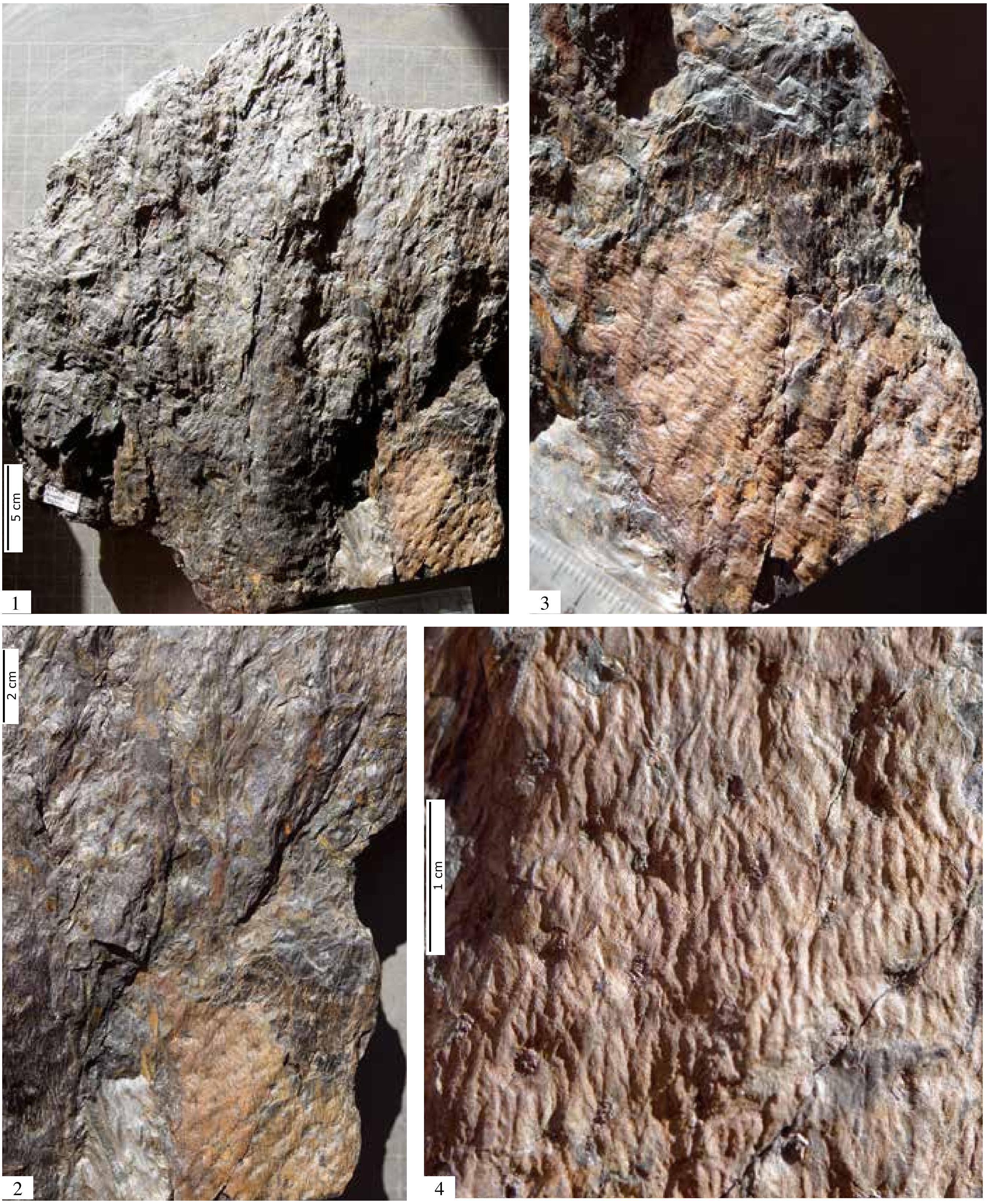


***Sigillaria parallela*. Leaves. Kronalm (Upper Carboniferous)**

1. Various leaves (KRON 202); 2–3. Single leaf with detail of midrib (KRON 260); 4. Detail of leaves (KRON 204); 5. Various rotting leaves (KRON 214); Coll. Wachtler, Dolomythos Museum, Innichen.

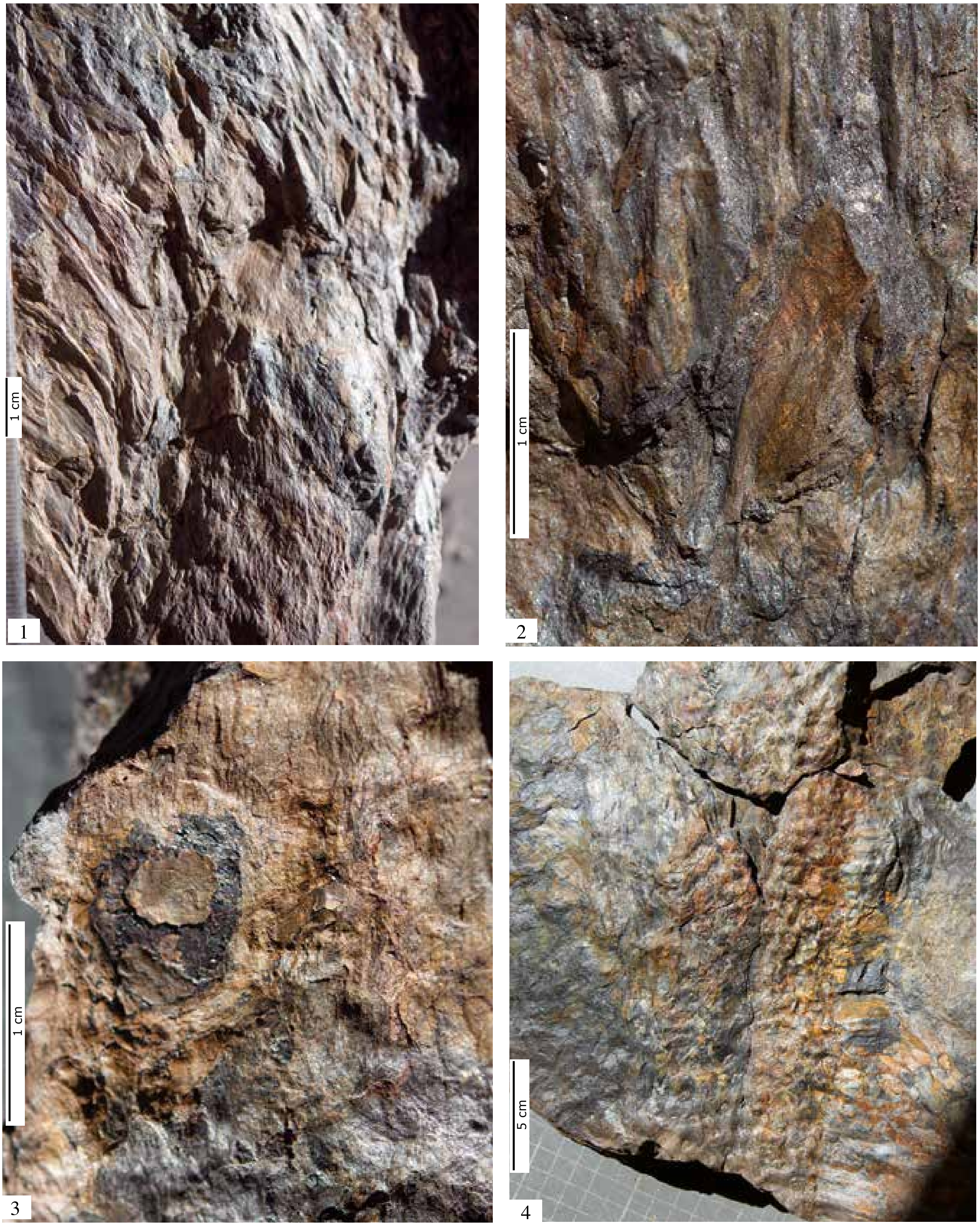
***Sigillaria parallela*. Naked sporophyll cones. Königstuhl (Upper Carboniferous)**

1–2. Dividing apex with the leaf scars of the sporophylls (KOEN 291, KOEN 215); 3–4. Three-dimensional trunk parts with abscission scars of the sporophylls (KOEN 154, KOEN 142); 5. Detail of the microleaflets which basally envelop the sporophylls (KOEN 207); Coll. Wachtler, Dolomythos Museum, Innichen.



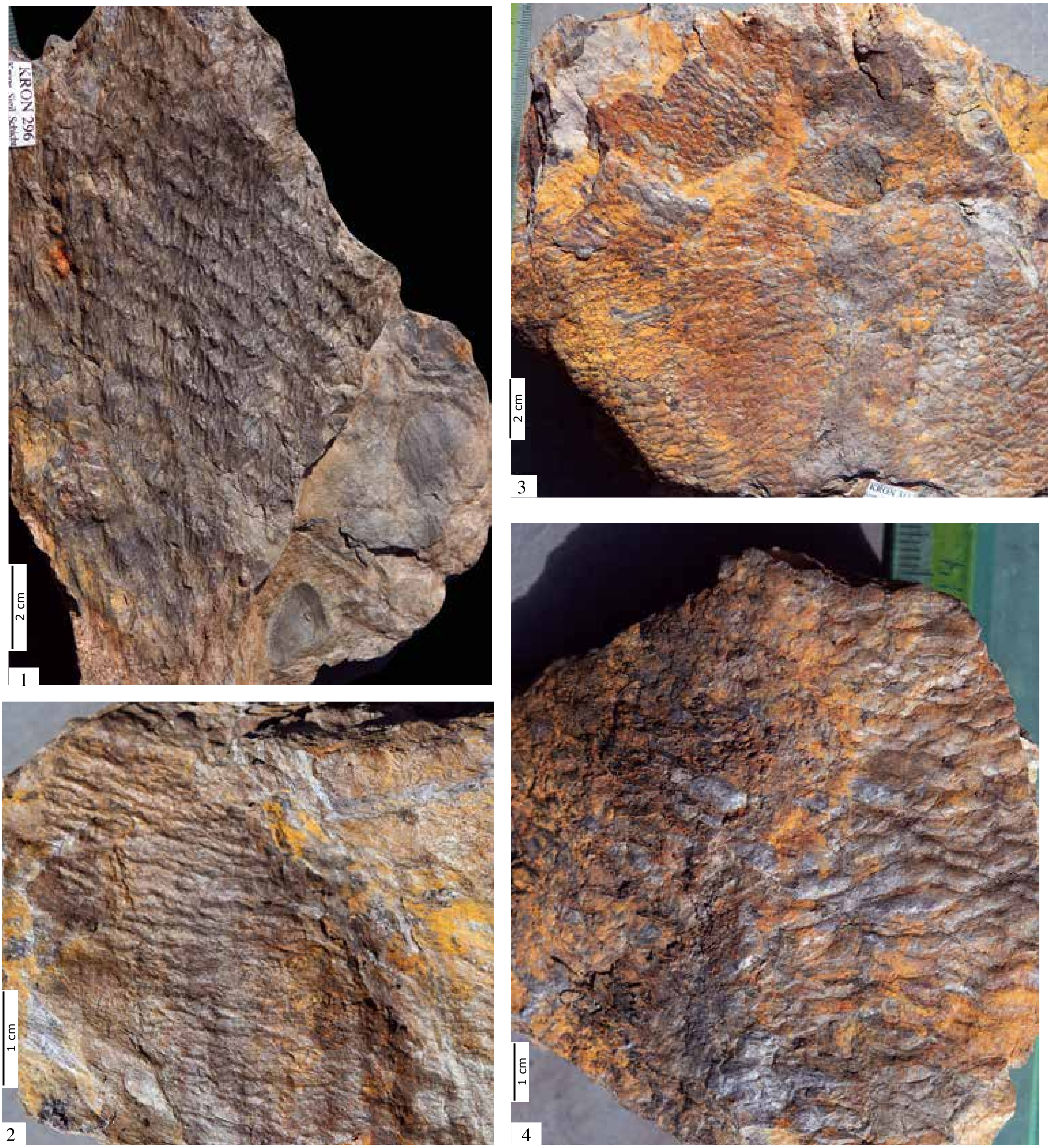
***Sigillaria parallela.* Scar cushions of shed sporophylls. Königstuhl(Upper Carboniferous)**

1. Aggregation of sporophyll cones; 2. Details of two cones with attached sporophylls; 3. Details of the micro-leaflets encasing the sporophylls at the leaf base; 4. Details of micro-leaflets and elongated cushions as remnants of shed sporangia (KOEN 235, neotype); Coll. Wachtler, Dolomythos Museum, Innichen.



***Sigillaria parallela*. Strobili (Upper Carboniferous)**

1–2. Part of a sporophyll cone. Sometimes scars from fallen sporangia can be seen, sometimes immature sporophylls are still attached to the trunk (KOEN 231); 3. Detail of a megasporophyll, which is surrounded by sterile dwarf leaves (KRON 181); 4. Dividing sporophyll cone and details of sporophylls (STANG 87); Coll. Wachtler, Dolomythos Museum, Innichen.



***Sigillaria parallela*. Sporophyll scars. Kronalm (Upper Carboniferous)**

1. Apical part of sporophylls separated by scar cushions, as well as several macrosporangia on the right side (KRON 296); 2. Sporophyll cones with elongated cushions of shed sporophylls (KRON 265); 3. Forking crest with sporophyll scars (KRON 311); 4. Two-part infructescence (KRON 304); Coll. Wachtler, Dolomythos Museum, Innichen.

wherein the *Sigillaria* occur in bulk. Some of these ash layers are 30–40 cm thick. They often contain many isolated *Sigillaria s*porophylls, with all other plant families such as ferns or horsetails receding in the background. This applies to all the fossil-rich sites on the Königstuhl, Stangalpe and the Kronalm.

Hence, the assumption arises that the giant clubmoss, especially the *Sigillaria* forests, cyclically became dominant. Due to recurring periods of drought or too many old stands, these trees died off on a large scale, as a single lightning strike was enough to set large areas of land on fire.

Such wildfire catastrophes caused not only a local devastation but could also spread over large landmasses and continents and thus change the global climate over long periods of time. Only after some time did the vegetation gradually recover; the megasporangia of the *Sigillaria*, with their hard shells, perhaps even needed such cataclysms to make their seedlings develop. The same assumption applies today to the giant sequoias (*Sequoiadendron giganteum)* of North America, whose cones often only open after bushfires. The role of such catastrophes in the world's climate has to be studied in more detail, but these mega-wildfires may have had a global impact via carbon dioxide exposure and heat output alone.

Soon after, since there was a general extinction of the giant clubmoss and a prolonged cold period, even in the vicinity of the equatorial region, the Carboniferous-Permian crisis, likely caused by both ice ages in the southern Gondwana hemisphere and the all-destroying forest fires in the tropics, perhaps drastically changed the global climate.

What we know about the *Sigillaria* seed clubmoss

Unknown ancestor between Devonian and Carboniferous: The giant *Sigillaria* appeared out of nowhere as mighty trees at the beginning of the Carboniferous, and they gave their place to the gymnosperms at the beginning of the Permian. They survived the Triassic as dwarfish plants, only to disappear from the scene towards the end of the Triassic.

Characteristic mega- and microsporophylls: Their main feature is their heterosporous infructescence, composed of a megasporophyll with a single, almost circular macrosporangium in the lower part, and in the upper part of the fructification somewhat elongated microsporophylls with a large number of microspores. Therefore, they can be referred to as a seed clubmoss. In this they differ from the homosporous *Lepidodendron* or today's *Lycopodium.* It can be assumed that despite their similar appearances, *Sigillaria* and *Lepidodendron* are not closely related and their splitting off must have taken place as early as the Lower Devonian.

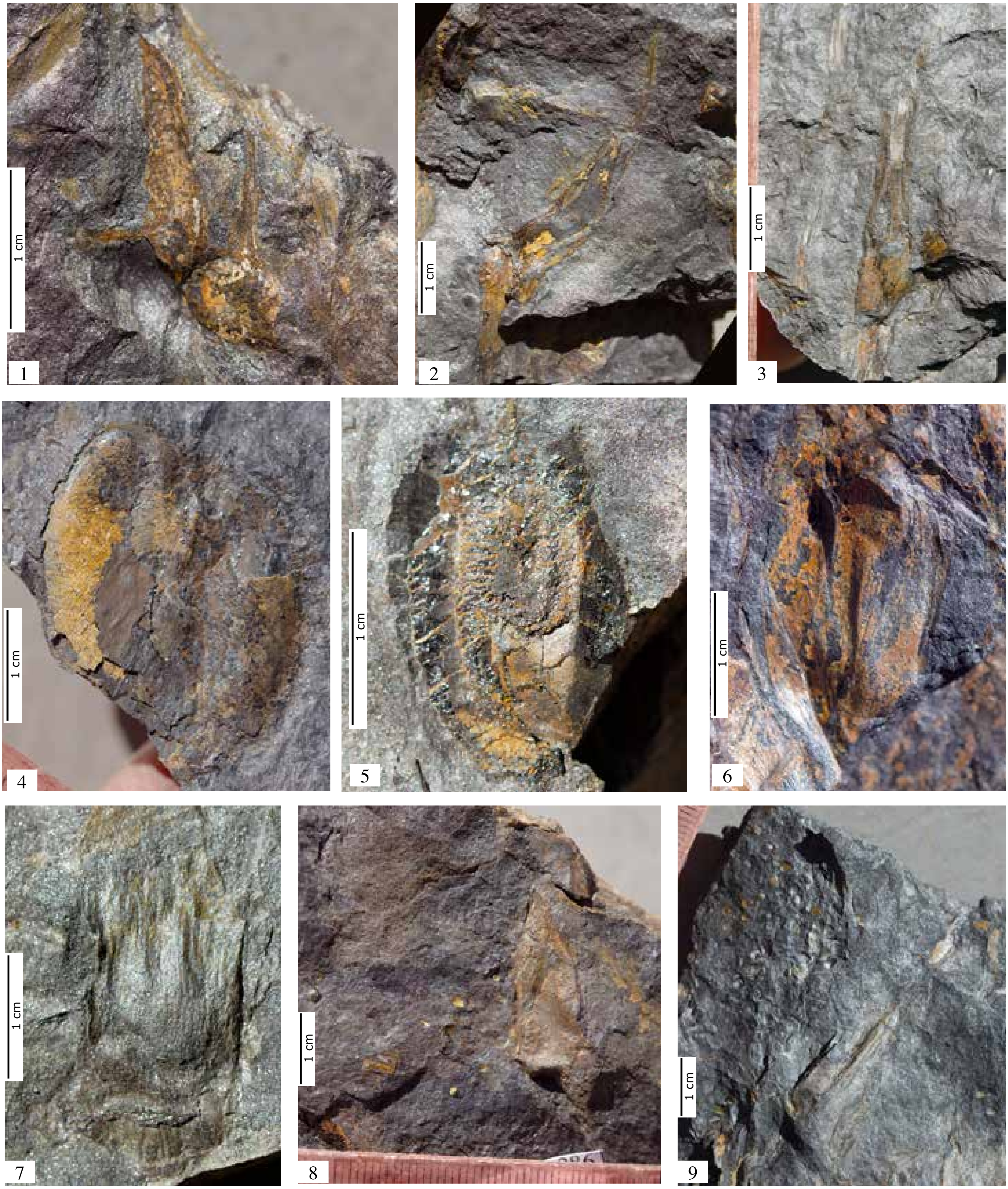
Typical leaf cushions: The fallen leaves of *Sigillaria* left scars that were round, only a little wider than they were high and had two–three vascular bundles in the middle. This was one of the features from that distinguished this clubmoss from the other common Upper Carboniferous lycophyte, *Lepidodendron,* whose leaf cushions were taller rather than wider.

Composite Stem Construction: The seedlings initially developed a single vascular bundle, a protostele, composed of surrounding divided leaf bases. These branched continuously into plectostelae. The trunks of the Sigillariaceae, thus, consisted of multiple aggregations of plectostelae. This enabled them to form a compact trunk consisting of many fused individual branches. Overall, one could speak of a bark trunk composed of several layers that were ridged in the basal part of the trunk.

Strong chlorophyll formation: In the upper halves of the trunk, the Sigillariaceae were densely covered with narrow, elongated leaves that reached up to 50 cm and had a strong central rib. This pattern continued on the forking side branches. The leaves themselves largely resembled those of *Lepidodendron,* making a clear assignment difficult.

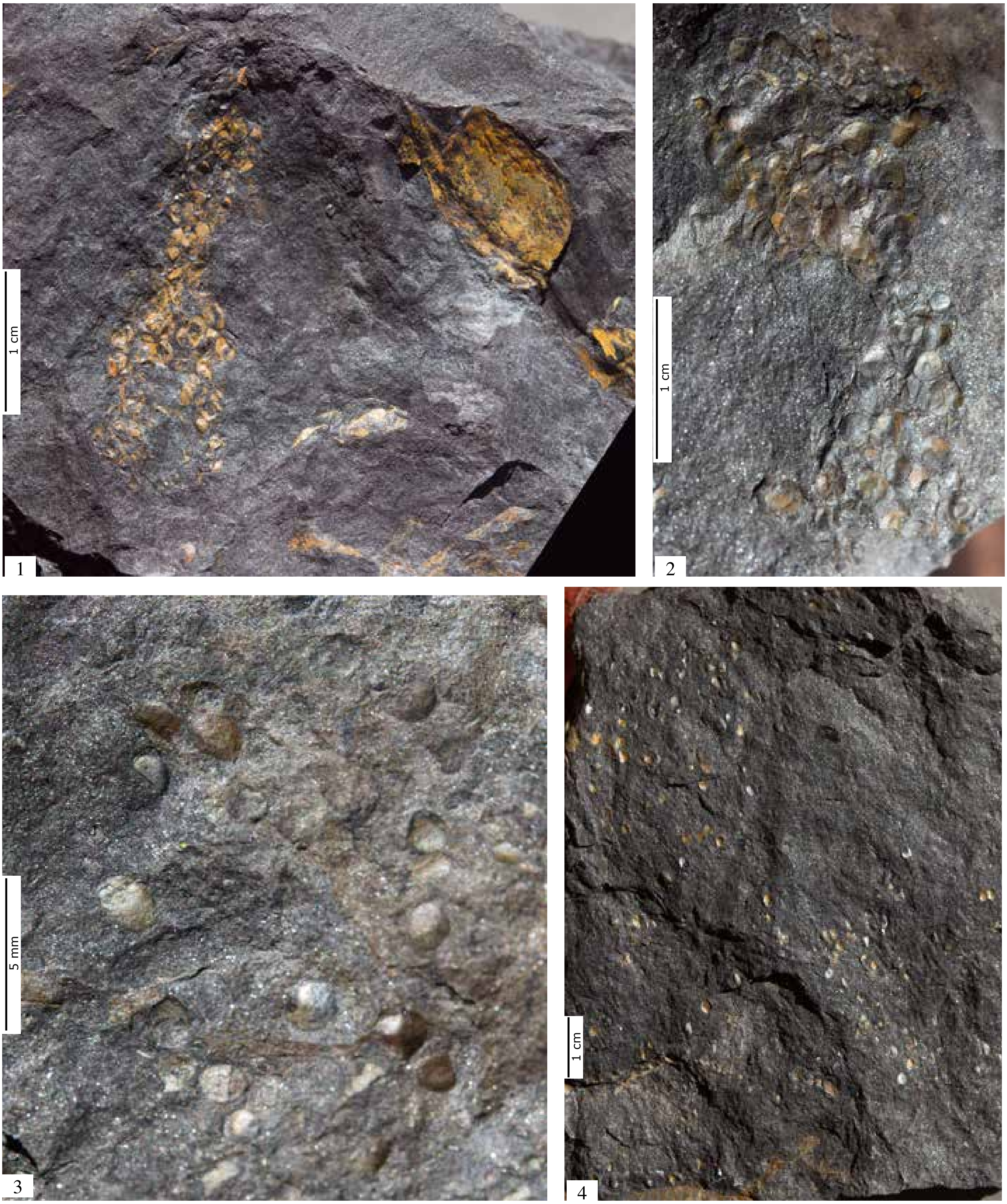
Huge wildfires due to rotting Sigillarias: Again and again, devastating wildfires – that probably affected large areas of the world's continents – occurred, probably due to prolonged dry seasons combined with overripe *Sigillaria.* In fact, massively charred strata associated with *Sigillaria* can be found everywhere.

Impact on the world climate: The abovementioned forest fires likely had an impact on the environment by emitting record



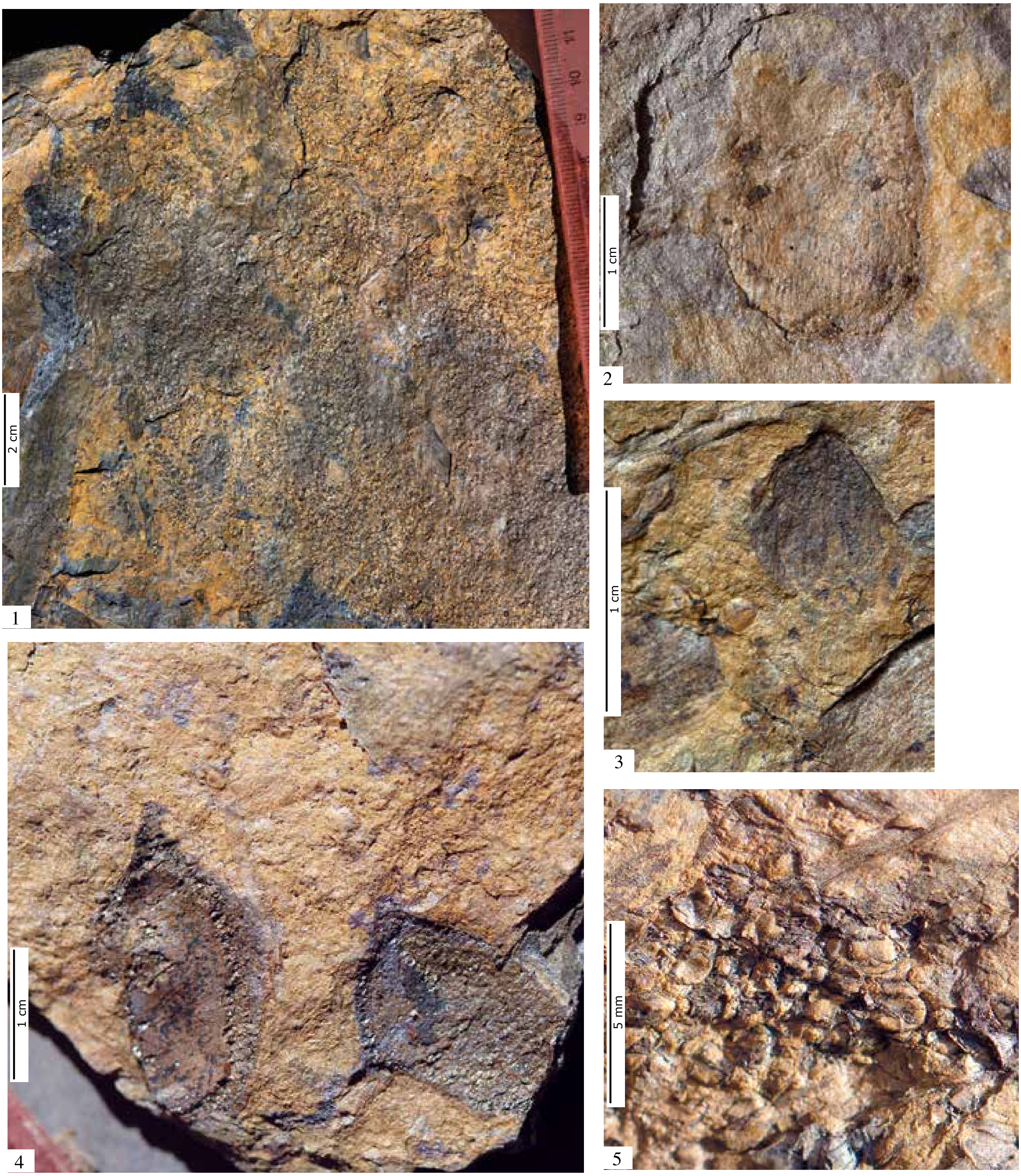
***Sigillaria parallela*. Sporophylls. Königstuhl (Upper Carboniferous)**

1. Two sporangia (side and front views) (KOEN 232); 2. Side view of a macrosporophyll with bract (KOEN 295); 3. Detail of a microsporophyll (KOEN 230); 4–6. Details of macrosporophylls (KOEN 185, KOEN 191, KOEN 145); 7–9 Details of microsporophylls with scattered microspores (KOEN 197, KOEN 286, KOEN 238); Coll. Wachtler, Dolomythos Museum, Innichen.Museum, Innichen



***Sigillaria parallela*. Microsporangia. Königstuhl (Upper Carboniferous)**

1. Cluster of microsporangia near a microsporophyll on the right side (KOEN 285); 2. Scattered microsporangia (KOEN 204); 3. Details of individual microsporangia with triradiate ornaments (KOEN 241); 4. Carpet of microsporangia (KOEN 303); Coll. Wachtler, Dolomythos Museum, Innichen.



***Sigillaria parallela*. Microsporangia. Kronalm (Upper Carboniferous)**

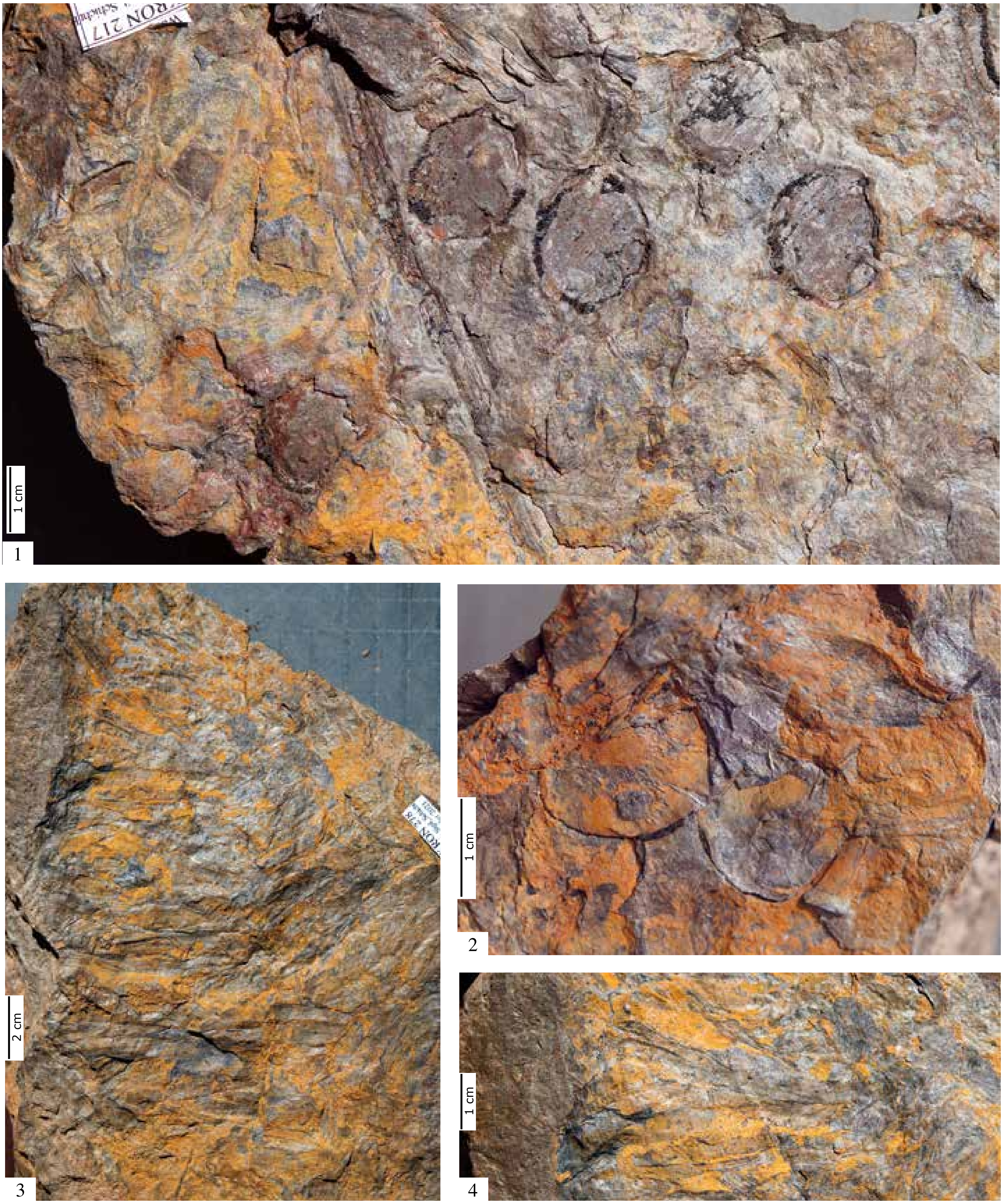
1. Carpet of microsporangia and some isolated microsporophylls (KRON 275); 2–4. Microsporophyll with released microsporangia (KRON 181, KRON 242, KRON 341); 5. Details of microsporangia, with triradiate ornaments (KRON 218); Coll. Wachtler, Dolomythos Museum, Innichen.

***Sigillaria parallela*. Microsporangia. Kronalm (Upper Carboniferous)**

1. Carpet of microsporangia (KRON 212); 2–3. Carpet of microsporangia and view of a microsporophyll (KRON 210); 4. Details of the microsporangia with excellently preserved proximal triradiate ornaments (KRON 208); 5. Carpet of microsporangia and the view of a microsporophyll (KRON 275); Coll. Wachtler, Dolomythos Museum, Innichen.

Sigillaria parallela. Megasporangia. Kronalpe (Upper Carboniferous)

1. Carpet of megasporangia (KRON 314); 2. Seedling with attached megasporangia (KRON 224); 3–4. Megasporangia (KRON 271, KRON 217); 5–7. Single megasporangia (KRON 358, KRON 305, KRON 279); Coll. Perner, coll. Wachtler, Dolomythos Museum, Innichen.



***Sigillaria parallela*. Megasporangia. Kronalm (Upper Carboniferous)**

1. Carpet of macrosporangia (KRON 217); 2. Various megasporangia on one plate KRON 257); 3–4. Cone with macrosporophylls and detail of a sporophyll (KRON 278); Coll. Perner-Wachtler, Dolomythos Museum, Innichen.

The Carboniferous *Sigillaria* Cycle: The Growth

On the left some seedlings are growing, in the middle there are mature specimens with sporophyll cones and on the right are the details of the macrosporangia and microsporangia.

amounts of carbon dioxide, and they may have affected wildlife as well.

Extinction of the giant clubmoss: Towards the end of the Carboniferous, there must have been massive climate changes due to various circumstances, including the effects of the Ice Age in the Southern Hemisphere. The time of the great lycophytes was coming to an end, while the now-appearing gymnosperms offered better survival conditions.

Bonsai clubmoss in the early Triassic: Surprisingly, almost all giant clubmosses survived, in dwarf forms, into the Triassic and experienced a brief boom in this period. This is true for *Lycopia* as a descendant of *Lepidodendron,* for *Eocyclotes* as a descendant of *Eurhytidolepis* or *Chaloneria*, and for *Sigillcampeia* as a descendant of *Sigillaria.* However, most of these died out by the end of the Triassic.

References

Álvarez-Vázquez, C. , Wagner R., 2014. Middle Pennsylvanian) of the Maritime Provinces, Canada, Atlantic Geoscience Society, vol. 50, pp. 167–232, Nov. 2014.

Berger, W. 1960. Neue Funde von Oberkarbonpflanzen in den Auernigschichten (Kärnten). – Verh. Geol. BA, S. 253–261, Klagenfurt.

Bouè A. 1835. Constit. geolog. des provinces illyriennes. —Memoires de la Societes geologique de Paris, II. Teil: 53—55

Brongniart A., 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux des terrains de sédiment supérieur en particulier. Soc. Philom., Bull., pp. 25-28 et Mémoires Du Muséum d'Histoire Naturelle 8: 203–240

Brongniart, Ad. , 1836 - Histoire des végétaux fossiles ou Recherches botaniques et géologiques sur les végétaux renfermés dans les diverses couches du globe (atlas), table 1, p. 166 p

Eggert, D.A. 1961. The ontogeny of Carboniferous arborescent lycopsida. Palaeontographica, Abteilung B 108, 43-9

Fritz, A., Boersma, M., 1988. Revision pflanzlicher Großreste aus dem Oberkarbon der Karnischen Alpen: Sammlung Höfer 1869- - Carinthia II, 172/92, 109-152, Klagenfurt

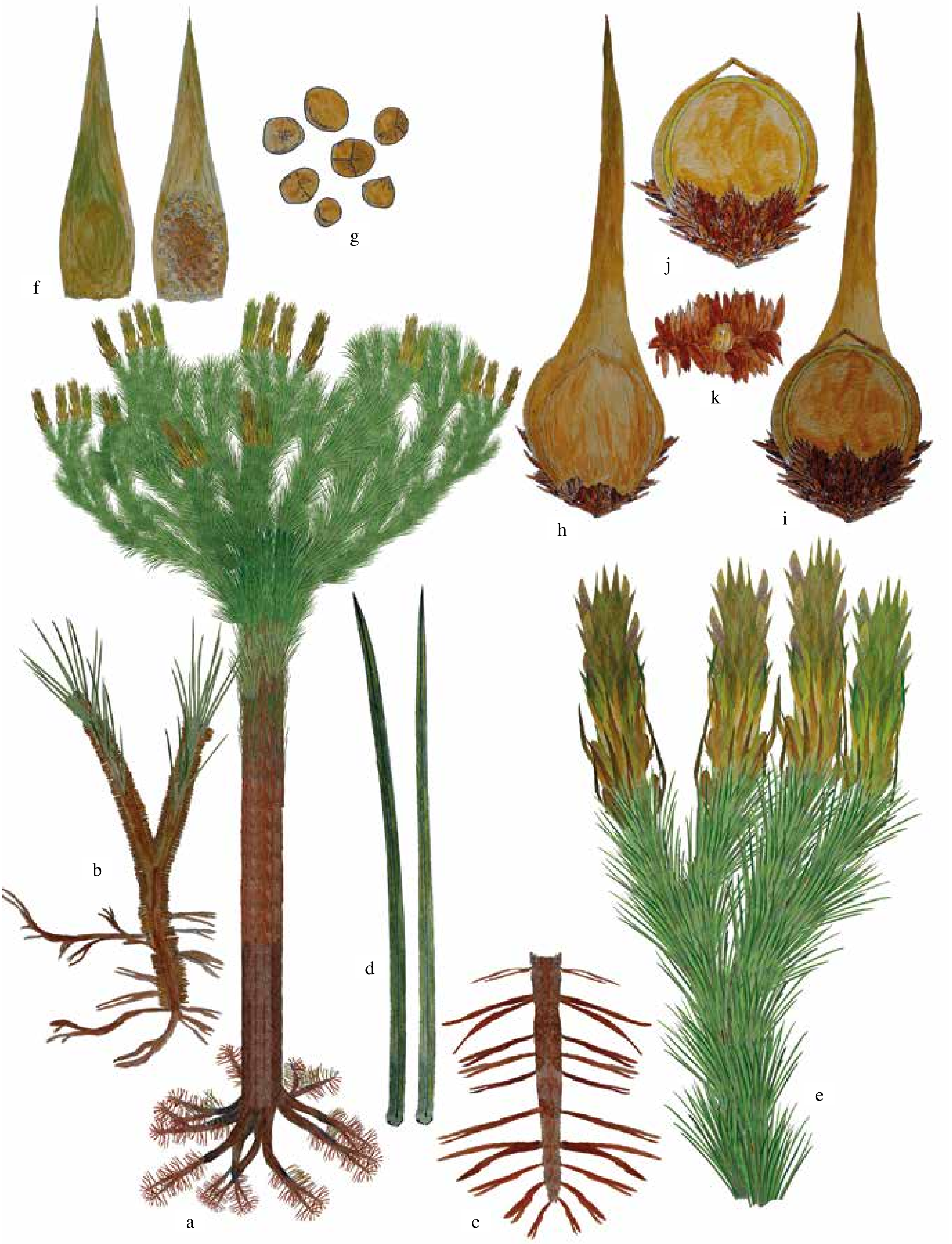
Fritz, A., M. Boersma, Krainer, K. 1990. Steinkohlenzeitliche Pflanzenfossilien aus Kärnten. - Carinthia II, Sonderheft 49, Klagenfurt

Fritz, A 1990. Zur Geschichte der paläobotanischen Forschung in Kärnten Carinthia, II. Jahrgang 100, S. 181-184 Klagenfurt

Hohenwart, v. S. 1783. Tagebuch einer Reise nach der

The Carboniferous *Sigillaria* Cycle: Maturity and Obsolescence

The Carboniferous *Sigillaria* Cycle: Fire Disasters



Sigilaria parallela. Reconstruction of a maturing tree (Upper Carboniferous)

a. Entire tree with roots and sporophyll cones in flower; b. Seedling; c. Root; d. Leaves (abaxial and adaxial); e. Strobilus; f. Microsporangia (abaxial and adaxial) g. Microsporangia; h. Macrosporangia abaxial side; i. Macrosporangia (adaxial side); j. Single Macrosporangium without bracts; k. Details of the encasing micro-leaflets evolving at the base of the sporangial abscission points.

***Sigilaria parallela*. Reconstruction of a dead tree (Upper Carboniferous)**

a. Entire tree with roots and bare sporophyll cones; b. Tree with outer bark and a view of the trunk core; c. Tree with shed leaves; d. Side branches with abscission scars and a view of the inner parts of the trunk; e. Side branches with leaf cushions; f. Side branch with leaf scars; g. Branchlet of last order; h. Leaf cushion; i. Side branch with dead fertile tuft; j. Leaf cushions of sporophylls; k. Leaf cushions of microsporophylls with sterile bracts; i. Mature microsporophyll with shed microsporangia; m. Single leaf cushion.

Stangalpe unweit Turrach in Steyermark, vom Jahre 1779. Fragmente zur mineralogisch und botanischen Geschichte Steyermarks und Kärnthens. 1:19—33

Kabon, H., 1997. Eine fossile Flora aus dem Nötscher Karbon. - Carinthia I I , 187./107. Jahrg.: 479-48

Kabon H. Amerom H. W.J., 1999. Neue fossile Floren aus dem Nötscher Karbon (1. Teil) 637- 672, Carinthia II

Kabon, H., Iglseder, C., 2019. Fossile Floren der Stangnock-Formation in den Gurktaler Alpen (Turracher Höhe, Nesselbachgraben, Reißeck, Frauennock). – In: Griesmeier, G.e.u. & Iglseder, C. (Eds.): Arbeitstagung 2019 der Geologischen Bundesanstalt–Geologie des Kartenblattes GK25 Radenthein-Ost, 55–83, Wien

Kandutsch, G., Wachtler, M., 2012. Fossile Pflanzen der Frühen Trias aus den Gailtaler Alpen, Carinthia II, pp. 71-80, Klagenfurt

Koehne, W. 1904. Sigillarienstämme, Unterscheidungs-merkmale, Arten, geologische Verbreitung, Ausgabe 43 von Abhandlungen der Königlich preussischen geologischen Landesanstalt, 72 Verlag S. A. W. Schade

Krainer, K., 1990. Zur faziellen Entwicklung Pflanzen-fossil-führender Oberkarbon- und Unterpermsedimente Kärntens.- In: FRITZ, A. ßOERSMA, M. & KRAINER, K. (1990): Steinkohlenzeitliche Pflanzenfossilien aus Kärnten.- Carinthia II, 180/100, 109- 1 32, Klagenfurt

Kustatscher, E., Nowak, H., Opluštil, S., Pšenička, J., Simonetto,L., 2019. The Carboniferous flora of the Carnic Alps: state of the art - La flora Carbonifera delle Alpi Carniche: lo stato dell’arte, Gortania Geologia, Paleontologia, Paletnologia 40 Udine, 10.XII.2019 ISSN: 2038-0410

Perner T., Wachtler M., 2013. The Carboniferous-Permian (Gzhelian/Kasimovian) Flora from Niederhausen (Rheinland-Pfalz, Germany), pp. 3-11, Editors: Dolomythos Museum, Innichen, South Tyrol, Italy, Oregon Institute of Geological Research, Portland, OR, (USA), ISBN 978-88-908815-1-0, Innichen, Italy

Schönlaub H.P., Hubmann B., 2002. Die Cellonetta-Lawinenrinne und die Pflanzenfundpunkte der Kronalpe (Karnische Alpen) 20-44, Berichte des Institutes für Geologie und Paläontologie der Karl- Franzens-Universität Graz, Band/Volume: 5

Sternberg, K.M., 1820-1838.Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt: v. I II, Regensburg und Prag. gedruckt bei Christoph Ernst Brenck’s Wittwe, 1825-1833

Stur, D., 1871. Geologie der Steiermark. - Geogn.-montan. Verein Steiermark, Graz

Unger, F. 1840. Ueber ein Lager vorweltlicher Pflanzen auf der Stangalpe in Steiermark. – Steiermärkische Zeitschrift, N.F., 6, 1, 140–153, Graz

Unger, F. 1847. Chloris protogaea. Beiträge zur Flora der Vorwelt. – 149 S., Wilhelm Engelmann, Leipzig

Unger, F., 1852. Versuch einer Geschichte der Pflanzenwelt, Verlag Wilhelm Baumüller, Wien

Unger, F. 1870. Anthracit-Lager in Kärnten. – Sitzungsber. Österr. Akad. d. Wiss., Bd. 60, Jg. 1869, Heft 6–10: 777–794, Wien

Wachtler, M., 12/2011. Lycophyta from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, Innichen. p. 165 - 211

Wachtler M., 2013. Protoconiferophyta from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany), pp. 48-60, Editors: Dolomythos Museum, Innichen, South Tyrol, Italy, Oregon Institute of Geological Research, Portland, OR, (USA), ISBN 978-88-908815-1-0, Innichen, Italy

Perner T., 2013. *Wachtlerina bracteata* a new conifer from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany), pp. 61-71, Editors: Dolomythos Museum, Innichen, South Tyrol, Italy, Oregon Institute of Geological Research, Portland, OR, (USA), ISBN 978-88-908815-1-0, Innichen, Italy

Wachtler M., 2016. A strange rising of the lycophyta in the European Triassic. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 2: Lycopods, horsetails, ferns, Dolomy- thos Museum, Innichen, South Tyrol, Italy, p. 3-16

Wachtler M., 2016. *Sigillaria*-Lycopods in the Triassic. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 2: Lycopods, horsetails, ferns, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 3-16

Wachtler M., 2021. *Eocyclotes alexawachtleri.* A New Arborescent Lycopod Family from the Early- Middle Triassic; p. 1-10; In Wachtler M., Wachtler N. (eds.): The Upper Triassic Raibl Cataclysm and its impact on the plant world. ISBN 978-88-944100-5-1

Wachtler, M., 2016. Bärlapp-Gewächse aus dem deutschen Unteren Keuper (Oberes Ladin, Mitteltrias) von Ilsfeld), S. 14-21 in Wachtler M., 2016. The Middle Triassic Flora of Ilsfeld (Germany) Ladinian, Erfurt Formation - Die mitteltriasische Flora von Ilsfeld (Deutschland) Ladin, Erfurt-Formation, Published by Dolomythos Museum, Innichen, South Tyrol, Italy

Zwanzinger, G.A. 1872. Die urweltlichen Pflanzen Kärntens nach ihrem Alter und ihren Lagerstätten verzeichnet. Carinthia II 62: 97-104

Zwanzinger, G.A. 1876. Die urweltlichen Pflanzen Kärntens nach ihrem Alter und ihren Lagerstätten verzeichnet. Jahrb. des Naturhist. Landesmuseums Kärnten 12: 71-90

Zwanzinger, G.A. 1891. Die Steinkohlen-Flora der Kronalpe und ihre Stellung jene der Stangalpe, von Bleiberg, Assling und der Wurmalpe bei Kaisersberg nächst Leoben. Carinthia II 81: 91-5

Carboniferous Fossil Floras from the Eastern Alps

Edited by Michael Wachtler and Nicolas Wachtler

Summary

The many and rich sites of fossil plants from the Upper Carboniferous period in the Eastern Alps have long aroused the interest of the local population and even more of researchers. Nevertheless, most of the sites are largely unexplored. Most sites are dominated by *Sigillaria*, in minority *Lepidodendron* lycopods, several *Calamites* horsetails and a variety of ferns, some of which could be defined as seedferns. Due to the large number of Sigillaria's, it was possible for the first time to obtain detailed information about this engimatic lycophyte, and even the variety of highly developed and well-preserved ferns, especially the Osmundaceae, Marattiales and tree ferns, offered the opportunity to learn more about their evolution.

With 600 photos and drawings

Editor: Dolomythos-Museum
39038 Innichen-San Candido, P. P. Rainerstr. 11 (BZ), Italy
Registration 36542 from 24/04/2021 - ISSN 2974-7376
Editor in chief Michael Wachtler
e-mail michael@wachtler.com
www.dolomythos.com

Euro 98,00
Pages 176